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SPECIES COMPOSITION AND FOREST STRUCTURE OF TREE COMMUNITIES IN FOUR PERMANENT FOREST MONITORING PLOTS IN THE TA'U UNIT OF THE NATIONAL PARK OF AMERICAN SAMOA

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INTRODUCTION AND BACKGROUND

The island systems of American Samoa represent a unique opportunity for forest conservation and ecological research. Forest covers the majority of the five main islands of Tutuila, Aunu'u, Ofu, Olosega and Ta'u. Recognizing this potential, the National Park system of the United States and the government of American Samoa established the National Park of American Samoa (NPSA), including both terrestrial and marine features of the islands of Tutuila, Ofu and Ta'u. These NPSA units contain excellent representatives of the natural ecosystems of American Samoa for long-term preservation, education and research.

Long-term management of forest ecosystems requires a detailed understanding of both the resources contained in the Park, as well as forest dynamic processes over time. Long-term monitoring is generally viewed as an appropriate way to capture both the static features of natural ecosystems as well as the dynamic processes within those ecosystems. Permanent forest monitoring plots are important for an understanding of the ecological processes that take place in a forest. Basic measures of tree diversity, forest structure, tree growth, and forest turnover are important parameters to monitor ecological processes in a dynamic environment. Over the long-term, the impacts of large-scale disturbances such as hurricanes and global climate change can be measured using permanent sample plots (hereafter, plots). Moreover, the impacts of human activity, conservation, and even invasive species can be addressed through a set of plots.

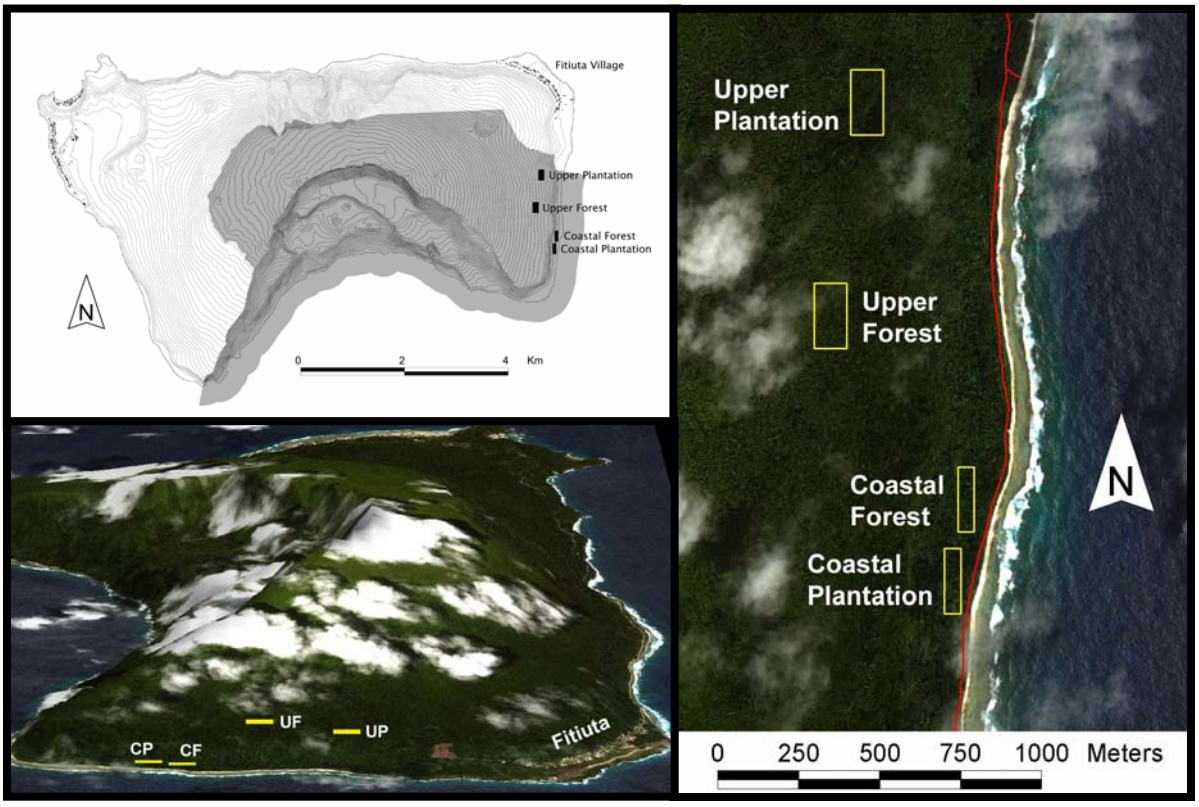
In the late 1990s, three 1.2-ha long-term forest permanent sample plots were established in the Tutuila unit of the NPSA (Webb and Fa'aumu 1999). A fourth plot was established outside the NPSA on Tutuila. However, there has been no effort to establish plots in the Ta'u unit. Therefore, establishing a set of plots on the island of Ta'u is an important step in the long-term conservation, management, education and research agenda of the National Park. This document presents the principal activities and results of field work to establish forest plots in the Ta'u unit of the NPSA.

METHODS

Site description

The volcanic island of Ta'u is the youngest island in the Samoan archipelago, formed approximately 300,000 ybp (Nunn 1998). The entire archipelago was formed above a geologic 'hotspot'. The hotspot is a massive pool of lava beneath the surface of the earth that produced the

Figure 1. Maps showing plot locations on Ta'u island. Top left: a topographic map with the Ta'u unit of the NPSA shown in gray. Bottom left, a three dimensional west-looking image. Right: a vertical view. The two color images are the output of a resolution merge between two IKONOS® images, (1 m and 4 m) resulting in a 1-m resolution image.



islands periodically as the plates moved over the hotspot in a westerly direction. Evidence for this formation is in the age of the islands, which follows a W-E pattern from oldest to youngest, with the island of Savai'i being the oldest at approximately 2.69 million years old (Nunn 1998).

Although the island of Ta'u was formed by the activity of one large volcano – Lata Volcano – two smaller lava volcanoes, Tunoa Volcano and Luatele Volcano, contributed to the NW and NE corners of the island. On the south side of the island, sheer cliffs from Lata summit (930 m asl) drop near-vertically to the Liu Bench and subsequently into the sea.

The Ta'u unit of the NPSA is located on the eastern portion of the island and extends from above Fitiuta village at the NE corner of the village past Luatele Crater and up to Lata. It extends to the southern edge of the island and includes portions of the Li'u Bench and southern coastline. It also covers the SE coastline, extending as far northward as the Saua village site,

Table 1. Description of tree-dominated vegetation (forest) types of Ta'u as defined by Whistler (1992).

Forest Type	Definition
Littoral forest	Dominated by *Barringtonia asiatica*, *Pisonia grandis* and *Hernandia nymphaeifolia*. Extends to about 60 m inland.
Dysoxylum lowland forest on coral rubble	Heavily dominated by *D. samoense*. In Whistler's 1980 survey of a 20 m x 50 m plot in the same site as the present *D. samoense* coastal forest, *D. samoense* had a relative basal area of 68%.
Dysoxylum lowland forest on talus slopes and cliffs	Located on cliffs and steep slopes along coasts. Dominated by *D. samoense* and *Hibiscus tiliaceus.*
Mixed lowland forest	Above cliff faces to about 35 m on the east side of the island. This 'undisturbed' forest type is generally absent from Ta'u because of agriculture and hurricanes. However, Whistler suspected that it would be dominated by *Syzygium inophylloides*.
Montane forest	Species-rich forest type beginning around 450 m elevation (lower on the east side, evidently). Dominated by *Astronidium pickeringii*, *Dysoxylum huntii*, *Cyathea* spp., and others.
Secondary forest	Forest recovering from both natural disturbance (hurricanes) and human-induced disturbances (agriculture). Dominated by *Alphitonia zizyphoides*, *Bischofia javanica*, *Dysoxylum samoense*, *Neonauclea forsteri*, *Pometia pinnata*, and *Rhus taitensis*, as well as the agroforestry species *Artocarpus altilis*, *Cocos nucifera*, and *Carica papaya*.

where the boundary is above the eastern escarpment (Figure 9). Within the Ta'u unit, several vegetation types have been described by Whistler (1992). Of those, only a few are dominated by trees (Table 1).

Site Selection

In general, the eastern side of Ta'u has been under traditional Samoan cyclical cultivation and (presumably) dispersed habitation for an unknown number of generations[1]. Clan-owned plantation land would usually be marked with several breadfruit and coconut trees on the borders, or with rock walls. In plantation areas, all forest trees would be cleared and crops such as taro and ta'amu would be planted for a few cycles depending on soil conditions and fertility.

[1] Historical information was gathered through informal conversations with High Chief Paopao and with several other citizens of Fitiuta village.

Although farmers would attempt to cut all trees, very large or unwieldy trees would be burned rather than cut. This technique, while generally successful, did not kill all the large trees on the land. Hence, some very large trees would inevitably remain on some farming land. Afterwards, bananas would be planted and root crops would be shifted to a new location.

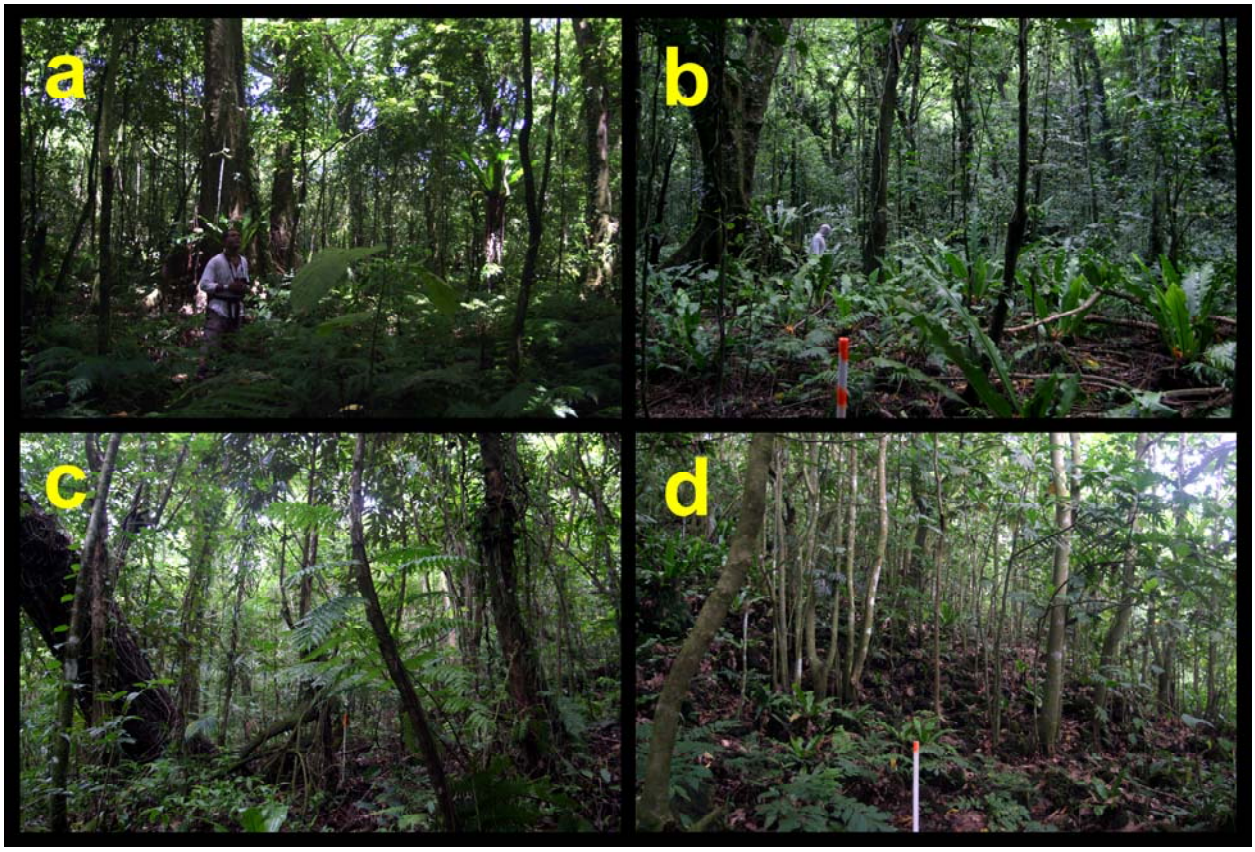
It was very difficult to piece together the specific cultivation history of eastern Ta'u prior to 1987. We learned that just before 1987, root crop cultivation was practiced in several locations above the escarpment until hurricane Tusi struck and destroyed the plantations. Subsequently, cultivation was shifted to Si'u. By 1991 / 92, root crop cultivation had shifted to Luama'a / Saua when hurricanes Ofa and Val struck in those years, respectively.

Although several informants revealed that they believed there were dispersed villages or houses above the eastern escarpment historically, it had not occurred in their lifetimes. So, although it is likely that there were dispersed settlements creating a matrix of forest and agriculture, it is unclear how long ago these existed. We were unable to find clear evidence of *fale* (traditional Samoan house) foundations in the forest during our field work, but we did not make a complete survey of the eastern part of the island.

Our field methods were undertaken through three general phases: initial reconnaissance, plot establishment, and tree survey. Reconnaissance hikes were taken in order to gather a specific understanding of the forest structure and composition of this NPSA unit before deciding on final plot locations. To achieve this, we undertook several days of reconnaissance hikes to evaluate forest conditions and assess the potential for plot establishment. Our reconnaissance hikes were done on several occasions and not only at the beginning of the field work. Our initial reconnaissance was done along the SE coastline to assess the potential for plot establishment in the coastal forest. This was followed by hikes to and above Luatele Crater from the old road above the quarry, and up to and following Laufuti Stream on Li'u Bench.

We first decided on establishing two 1-ha (50 m x 200 m) coastal plots at Lua amata: one in a relatively intact site described as *Dysoxylum* coastal forest by Whistler (1992), and a second in an area that clearly had beeN utilized as a plantation prior to the establishment of the NPSA (Figure 2). The *Dysoxylum* coastal forest (hereafter referred to as the Coastal Forest plot)

Figure 2. Photographs of three of the four sites selected for plot establishment: a and b, Coastal Forest (note abundant Asplenium nidus); *c, Upper Forest (note epiphytes); d, Upper Plantation (note abundant multiple-stemmed* Artocarpus altilis *trees).*



had many very large *Dysoxylum* and other native forest trees, as well as few or no plantation trees. Additionally, the bird's nest fern *Asplenium nidus* L. was very abundant on the forest floor and growing on rocks. In contrast, the plantation site (hereafter referred to as the Coastal Plantation plot) had fewer large trees and large populations of coconut and breadfruit trees. The soil of both plots was the Ngedebus variant, i.e. poorly weathered basaltic alluvium with coral rubble.

We established two 2-ha (100 m x 200 m) plots in forest near 200 m elevation, in an area generally known as Lalomaota (Figure 2). Evidently, Lalomaota was recognized as an area that contained a high density of maota trees, under which one could rest after the walk to the area, or after hunting or other work on the plantation. According to Whistler (1992), 'maota' refers to *D. huntii* on Ta'u, although on Tutuila, 'maota' refers to *Dysoxylum maota*. Since there is no *D. maota* on Ta'u, the Lalomaota reference may be to *D. huntii*. High Chief Paopao described

'maota' as a slow-growing, hard-wooded tree with short compound leaves. *D. huntii* leaves fit this description, although we do not know the growth rate or wood hardness.

The third plot is a regenerating plantation located at about 150 m elevation. We interviewed several people and they were all aware of extensive plantations above the escarpment, in approximately the same area where this plot was located. We are confident that this plot was established within the area described as old village plantations. This plot was named Upper Plantation.

The landscape is terraced to facilitate taro cultivation. This forest was dominated by a population of breadfruit trees, which appeared to be a well-established and regenerating population that had taken over previously cleared agricultural land. While native forest trees and regeneration were encountered during our initial reconnaissance, it was clear to us that this site was clearly dominated by the agroforestry species. We therefore took great interest in the area as a monitoring site, which will allow us to follow regeneration of the forest after abandonment since (presumably) 1987.

The fourth plot is located approximately 500 m south of the Upper Plantation, at approximately 200 m elevation. During our reconnaissance surveys we encountered this area and noted that it seemed to have the most complex structure on the eastern slope, which may suggest the least amount of disturbance from agriculture and/or natural processes. There were several old rock walls of about 1 m height in an uphill-downhill orientation in the area. These may have been boundary markers among households or villages. Despite the clear indication of human presence, we found no large plantation trees in the immediate vicinity; we did, however, encounter several seedlings of *Artocarpus altilis* in and near the plot. The area was also notable because of the presence of a massive *Calophyllum inophyllum* tree and many large trees of slow-growing species. Moreover, there was a robust epiphyte load. These features suggested that the area was the least impacted forest and would therefore make an excellent comparative plot to the Upper Plantation. This plot was named Upper Forest. The soil of the upper plots was the Pavaiai series, i.e. a very rocky soil underlain with lava flow.

GPS points for the NE corner of each plot using the UTM coordinate system (datum NAD83) are as follows: Coastal Plantation: E 670209, N 8424413; Coastal Forest: E 670251, N 8424663; Upper Plantation: E 669970, N 8425889; Upper Forest: E 669857, N 8425231.

1	21	41	61	81	101	121	141	161	181
2									
3									
4									
5									
6									
7									
8									
9									
10	30	50	70	90	110	130	150	170	190
11									
12									
13									
14									
15									
16									
17									
18									
19									
20	40	60	80	100	120	140	160	180	200

North

Figure 3. Numbering scheme of subplots in the permanent plots. Each subplot is 10 m x 10 m. This example is for the 2 ha upper plots (100 m x 200 m).

Plot establishment and survey

We established the plots using standard protocols designed and implemented for permanent sample plots around the world (Alder and Synnott 1992). The plots were established to measure 1-ha and 2-ha on the horizontal plane, with PVC tubes inserted into the ground every 10 m. We used a Suunto® KB-14 sighting compass (accuracy 0.17 degree) and Leica DISTO® laser distance meter (accuracy ±3 mm) to make the measurements. The KB-14 compass could not be calibrated for the large magnetic declination in American Samoa, so the plots were oriented towards magnetic north[2]. Subplots were numbered from 1 to 20 in the westernmost 'column', subplots 21 – 40 in the adjacent column, and so forth. The lowest subplot numbers in the column were always to the north (Figure 3).

[2] All plots were oriented so that the long axis was oriented N-S.

Figure 4. Some data collection methods. Top left: measuring DBH of large buttressed Dysoxylum samoense *tree. Top right: nailing tag into a double-stemmed* Syzygium inophylloides *tree. Lower left: measuring DBH and recording of a small* Ficus scabra *tree. Lower right: Using a laser meter to measure distance from a triple-stemmed individual to subplot corners.*

We encountered serious difficulty with 'magnetic anomalies' in all plots. These anomalies were shifts in the magnetic field that strongly affected the compass reading. These fields could change a compass reading by several degrees, leading to erroneous readings and difficulties in making straight plot lines. This may have been related to the magnetic orientation of minerals in the lava. We triangulated readings from other PVC tubes when necessary to make the plots as precisely measured as possible with our equipment.

When the plot framework was established, we surveyed every tree ≥10 cm dbh (diameter at 1.4 m height, avoiding stem irregularities). In each subplot, every stem was identified to species and measured for dbh using a standard diameter tape (Figure 4). For trees that branched

below 1.4 m height, including coppices, we measured, tagged and recorded each stem individually.[3] However, these stems were all recorded as belonging to the same individual.

Hibiscus tiliaceus is a scrambling shrub or tree, and it is not uncommon to find adventitious roots emerging from a vertical branch on a horizontal main stem. Moreover, large stems may also enter into the soil and set root. In effect, rooting of both branches and main stems could make those sections of the individual independent of the larger organism. When we encountered mature, adventitious rooting systems in *H. tiliaceus* beyond 1.4 m from the original base of the tree that would allow that portion of the individual to survive in the case of damage to the base of the tree, we considered it to be a unique individual. Any adventitious roots within 1.4 m of the base of the tree were considered to be part of that individual. Using this rule allowed us to make consistent decisions for our data collection. However, in our data an individual of *H. tiliaceus* does not necessarily refer to genetically distinct individuals. Our decision rule resulted in some redundant measurements of the same genets, although we have no idea of how much redundancy there was.

A unique numbered tag was nailed to the stem 20 cm above the dbh measuring point. The tags for this project were numbered from 1 to 1000. In the 2 ha plots there were more than 1000 trees in each plot, so trees 1000 – 1500 were given two consecutively-numbered tags (e.g. 001002), and trees 1500 – 1833 were given 3 tags (e.g. 001002003).

We included tree ferns (*Cyathea* spp.) in the survey. Tree ferns were included because they added an important element to the structure of the forest. However, we did not measure dbh because the diameter of tree ferns does not increase like dicotolydonous trees. However, we did map their locations and calculate their heights.

Heights of all trees and tree ferns were calculated using a Suunto® clinometer and measuring the angle to the top of the tree, to the first branch above 1.4 m, to the base of the tree, and by measuring the horizontal distance to the tree with the laser meter. The height of first branch was measured in order to add a new measure of forest structural complexity to our

[3] In many cases, where multiple stems were superficially fused or when multiple stems emerged very close together from the ground, it was difficult to determine whether those stems were from one genetically unique individual, or whether each stem was itself an individual. We examined every questionable case thoroughly, looking for evidence of a shared root system, which would indicate a coppice or vegetative sprout (e.g. root sucker). Where there was clear evidence of a shared root system, coppicing, or branching, we recorded those stems as belonging to one individual. When clear evidence was lacking, we recorded each stem as a unique individual.

Figure 5. Data collection duties were consistent for each team member throughout the course of the field work; such data collection requires serious concentration and commitment. Enamul Kabir, pictured below, was responsible for recording each of the >40,000 data points. Similarly, Martin van de Bult (not pictured) measured the heights of all stems, using a clinometer to measure three features of the >4100 stems. Maintaining team cohesiveness and morale is essential for accurate data collection, and when present can lead to high data collection efficiency and a low error rate. In a resurvey of these plots in 2005 after Cyclone Olaf, we detected a data collection error rate of less than 0.1%.

analysis. For tree ferns, the 'height of first branch' was the height of emergence of the lowest frond.

We constructed a map of all trees and tree ferns in the plots. Mapping was accomplished by measuring the distance of each individual to the NW and SW corner of the subplot and converting those measures into Cartesian coordinates (x,y) for the subplot, and then converting those coordinates to Cartesian coordinates for the entire plot.

The total field time to set up these four plots was 66 days. It is important to note that the core four-member team maintained consistency in work quality by having each member follow a specific data collection duty for the entire field period (Figure 5). There were several data points being collected simultaneously for each tree: tag number, dbh, species name, coordinates, tree height measurements, and any notes of interest (tree leaning, bark damage, etc). It was essential

that we maintained consistency as much as possible in terms of which person was communicating a particular piece of information to the data recorder. Thus, team members did not shift among work duties very much, so the overall team was able to maintain a high level of work efficiency as we evolved an effective data collection strategy.

Data analysis

After data entry, the data were cleaned by a thorough check. Any discrepancy was rectified by revisiting the tree in the field, resampling the individual, and changing the entry in the computer if necessary.

For the analysis, we differentiated between 'individuals' and 'stems'. A tree with several branches originating below 1.4 m was considered one individual with multiple stems. We calculated our diversity indices and tree densities (and derivatives of tree densities) based on individuals. Basal area measurements, however, included all stems of all species.

The similarity among plot species compositions was calculated using the Morisita-Horn Index of similarity, which is less influenced by species richness and sample size than other similarity indices such as the Jaccard Index or Sorenson Index (Magurran 1988). Diversity indices were calculated with the statistical ecology programs written by Ludwig and Reynolds (1988). We calculated three diversity indices aside from total richness: Simpson's λ (Simpson 1949), Shannon's H' (Shannon and Weaver 1949), and the modified Hill Ratio for evenness (Alatalo 1981).

To estimate the degree of clumping of trees in each plot, we calculated Ripley's K (Ripley 1981) for the entire tree community and the most important species. Ripley's K was calculated across a range of lag distances, from 1 – 25 m for the coastal plots and 1 – 50 m for the upper plots; in both cases we used 1-m lag distance intervals. We used the Splancs package (Rowlingson and Diggle 2004) adapted for the R language and environment (R Development Core Team 2005). In this paper we present the basic spatial analysis of whether the species exhibited clumping and if so, at what lag distances.

RESULTS AND DISCUSSION

Forest composition

In the total 6 ha, we encountered a total of 54 tree species, not including the tree ferns which we recorded as *Cyathea* sp. (Appendix 1). Several of the tree species in the plots are uncommon to rare in American Samoa. These include *Celtis harperi*, *Litsea samoensis*, *Crateva religiosa*, and *Euodia hortensis*. *Dysoxylum samoense* was the most abundant species across all four plots, followed by *Artocarpus altilis* and *Hibiscus tiliaceus*. However, there was substantial variation among plots in terms of composition and diversity.

A total of 18 species were found in the Coastal Plantation. This plot was dominated by *D. samoense*, with *Macaranga harveyana*, *A. altilis*, and *Cocos nucifera* of secondary importance (Appendix 1). In the Coastal Forest, we encountered 16 species. The plot was dominated by *D. samoense*, accounting for about 41% of all trees. Of secondary importance was *Diospyros samoensis*, *Sterculia fanaiho*, and *Pisonia umbellifera* (Appendix 1).

In the Upper Plantation, 26 tree species were recorded. This plot was heavily dominated by *A. altilis* and *D. samoense*, with *Ficus scabra* a distant third in importance (Appendix 1). There were 70 stems of *Morinda citrifolia*, several large *Spondias dulcis* trees, along with one *Carica papaya* stem and one *Syzygium malaccense* tree. In the Upper Forest, a total of 35 species were encountered. *H. tiliaceus* was the most common individual, followed by *Myristica inutilis* (Appendix 1). This plot contained good populations of *Trichospermum richii* and *Pometia pinnata*, both of which were absent from the NPSA plots on Tutuila (Webb and Fa'aumu 1999). This plot also contains *Celtis harperi*, *Litsea samoensis* and *Euodia hortensis*, which were uncommon in American Samoa and absent from the National Park plots on Tutuila.

Of particular interest was the finding of several non-native *Flueggea flexuosa* individuals in the Coastal Plantation and the Upper Forest. To date there have been no formal reports of *F. flexuosa* establishing in natural forest outside of homesteads, so these plots demonstrate that *F. flexuosa* can naturalize in native forests of American Samoa.

Table 2. Diversity indices of the four permanent forest plots, Ta'u.

Diversity Index	Coastal Plantation	Coastal Forest	Upper Plantation	Upper Forest
Richness	18	16	26	35
Simpson's λ	0.18	0.21	0.25	0.15
Shannon's H'	2.08	1.99	1.84	2.47
Modified Hill Evenness Ratio	0.65	0.59	0.58	0.51
Stem Density (number / ha)	459	327	588.5	633.5
Basal Area / Ha	23.78	31.42	27.23	29.27

Table 3. Morisita-Horn similarity indices among the four plots.

	Morisita-Horn Index of similarity		
	Coastal Plantation	**Coastal Forest**	**Upper Plantation**
Coastal Forest	0.779		
Upper Plantation	0.702	0.518	
Upper Forest	0.140	0.188	0.163

Diversity indices revealed that in addition to the highest species richness, the Upper Forest was most diverse in terms of Simpson's λ and Shannon's H' (Table 2). On the other hand, the modified Hill Ratio – which approaches zero as one species becomes increasingly dominant in the community – suggests that the species in the Upper Forest were the least evenly distributed. This is probably because of the heavy dominance of *H. tiliaceus* in the Upper Forest. The relatively greater dominance of *H. tiliaceus* over species ranks 2, 3, and 4 than in other plots resulted in a low evenness index.

Morisita-Horn Indices revealed high similarities between the Coastal Plantation and the Coastal forest (0.779) and between the Coastal Plantation and the Upper Plantation (0.702) (Table 3). Moderate similarity existed between the Coastal Forest and the Upper Plantation (0.518), and low similarity was exhibited between the Upper Forest and any of the other three plots (<0.200 for each). Thus, compositional similarities were greatest among the two lowest-diversity plots, with the least similarity between the highest diversity plot and any other plot.

Forest structure

Forest structure varied across the four plots. Tree densities ranged from 327 ha^{-1} in the Coastal Forest to 633.5 ha^{-1} in the Upper Forest (Table 2). The Coastal Plantation and Upper Plantation were intermediate, with 459 trees ha^{-1} and 588.5 trees ha^{-1}, respectively. Basal areas ranged from 23.8 m^2 ha^{-1} in the Coastal Plantation to 31.42 m^2 ha^{-1} in the Coastal Forest. The Upper Plantation and the Upper Forest plots were intermediate, with 27.2 m^2 ha^{-1} and 29.7 m^2 ha^{-1}, respectively. The Coastal Forest had few small trees, resulting in low tree density values, but massive *Dysoxylum* trees that accounted for 24.1 m^2 ha^{-1}, i.e. 76.6% of the total plot basal area (Appendix 1). Species ranks according to total basal area were generally similar to abundance rankings. *D. samoense* was first in three of the four plots, with *H. tiliaceus* ranking first in the Upper Forest.

A total of 372 trees in 31 species were multiple-stemmed (Table 4), which is 11.5% of all individuals, and 57% of the species. The coastal plots had proportionately fewer multiple-stemmed trees, 6.5% and 4.9% in the Coastal Plantation and the Coastal Forest, respectively. In contrast, 13.1% of the trees in the Upper Plantation, and 13.6% of the trees in the Upper Forest were multiple-stemmed. In terms of proportion of species with multiple-stemmed individuals, the numbers were consistent across plots. The Coastal Plantation had 9 species with multiple-stemmed individuals (50% of the total species), the Coastal Forest had 7 species (44%), the Upper Plantation 11 species (42%) and the Upper Forest 15 species (43%). Thus, whereas the number of trees with multiple-stems differed across sites, the proportion of species with multiple-stems did not.

Species that had notably high levels of multiple-stemmed trees included *A. altilis*, *Bischofia javanica* and *D. samoense* in the Upper Plantation, and *H. tiliaceus* and *Syzygium inophylloides* in the Upper Forest. However, for *A. altilis* and *D. samoense* it was very difficult to differentiate between multiple-stemmed individuals and genetically unique individuals that had established next to each other. It is most likely that multiple-stemmed trees in the Upper Plantation resulted from historical cutting during plantation management, such as with *B. javanica*.

Table 4. Frequency of individuals with multiple-stems in each plot.

	Coastal Plantation		Coastal Forest		Upper Plantation		Upper Forest		Total	
SPECIES	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
Alphitonia zizyphoides							2	1.9	2	1.8
Artocarpus altilis	11	18.0			57.0	12.2			68	12.9
Barringtonia asiatica	5	33.3	2	20.0					7	28.0
Barringtonia samoensis					2	11.8			2	11.8
Bischofia javanica					19	26	2	4.3	21	17.6
Cerbera manghas							1	16.7	1	16.7
Diospyros samoensis			2	5.1					2	3.4
Dysoxylum samoense	2	1.3	2	1.5	46	14.6	10	11.9	60	8.7
Elaeocarpus floridanus							1	2.9	1	2.9
Erythrina variegata			2	100.0					2	100.0
Ficus scabra					9	8.3			9	5.5
Ficus tinctoria			1	100.0					1	25.0
Flacourtia rukam							4	13.3	4	12.9
Flueggea flexuosa	1	11.1							1	5.6
Garuga floribunda					2	25.0			2	11.1
Hernandia nymphaeifolia	3	30.0							3	30.0
Hibiscus tiliaceus					3	8.8	121	27.9	124	26.6
Litsea samoensis							1	50.0	1	50.0
Macaranga harveyana	1	1.3							1	1.3
Macaranga stipulosa					2	66.7	1	4.5	3	12.0
Morinda citrifolia	1	14.3			8	11.4			9	10.0
Myristica inutilis							5	3.9	5	3.5
Neonauclea forsteri							4	12.9	4	11.4
Pipturus argenteus					1	5.6			1	4.8
Pisonia grandis	4	19.0							4	10.8
Pisonia umbellifera			5	15.2					5	15.2
Planchonella garberi							1	8.3	1	8.3
Rhus taitensis					5	45.5	6	6.7	11	11.0
Sterculia fanaiho	2	66.7	2	6.1					4	4.9
Syzygium inophylloides							12	12.8	12	12.8
Trichospermum richii							1	4.8	1	4.8
Sum	30		16		154		172		372	
Percent stems	**6.5**		**4.9**		**13.1**		**13.6**			**11.5**
Percent species	**50**		**44**		**42**		**43**			**57**

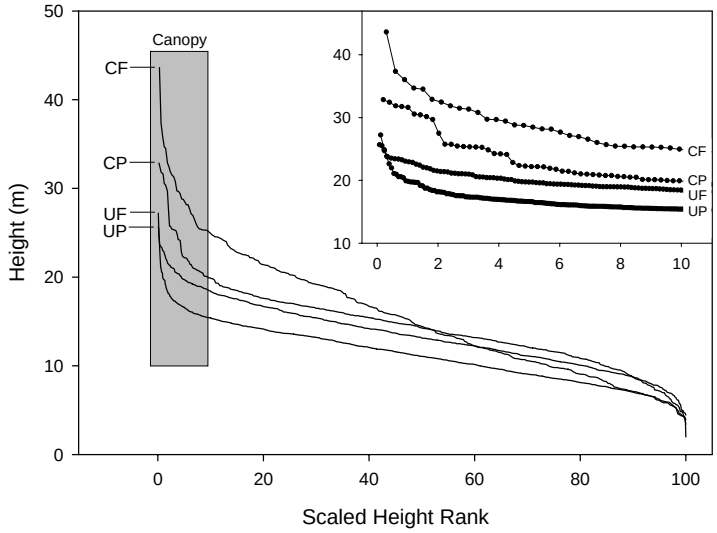


Figure 6. Rank-height diagrams for the four permanent plots, scaled to 0-100. The canopy was defined as the tallest 10% of all trees in the plot. The inset shows the rank height relationship for canopy trees only.

The Coastal Forest had the tallest canopy, which was defined as the tallest 10% of trees in each plot (Figure 6). The top 10% of trees were taller than 25 m in the Coastal Forest, 19.8 m in the Coastal Plantation, 18.3 m in the Upper Forest, and 15.4 m in the Upper Plantation (Figure 6 inset). These figures may not precisely measure the 'canopy height', which is the height of the upper contiguous tree crowns of a forest (Richards 1996). However, they can be considered general estimates of canopy height, and are accurate indicators of the difference in canopy heights among the plots. It is clear that the two coastal plots were taller than the upper plots. This difference becomes more evident if the comparison is made between analogous plots, where the Coastal Forest canopy was about 9.5 m taller than the Upper Forest, and the Coastal Plantation canopy was about 4.5 m taller than the Upper Plantation canopy.

The decline of the scaled-rank-height curves for the subcanopy was parallel for the Coastal Plantation, Upper Forest and Upper Plantation plots (Figure 6). This suggests that the plots had similar proportions of trees across the height spectrum. Vertical structural complexity of those three plots was therefore similar. However, the Coastal Forest curve declined at a faster rate than the other three plots. This indicates that the Coastal Forest had fewer mid-story trees relative to the other plots, suggesting a more simplified vertical structure than the other three plots. The simplified vertical structure was also evident with a lower proportion of trees with multiple stems (Table 4).

Table 5. The tallest 20 trees in each plot. In order to save space, the species coding system uses the first three letters of the genus name and the first three letters of the species name.

	Coastal Plantation			Coastal Forest			Upper Plantation			Upper Forest		
Rank	Species	DBH (cm)	Ht (m)	Species	DBH (cm)	Ht (m)	Species	DBH (cm)	Ht (m)	Species	DBH (m)	Ht (m)
1	PISGRA	100.5	32.8	DYSSAM	101.3	43.6	SPODUL	54.8	25.7	ALPZIZ	37.4	27.2
2	PISGRA	134.3	32.4	DYSSAM	63.7	37.3	SPODUL	67.2	25.5	SYZINO	38.0	24.9
3	DYSSAM	79.0	31.8	DYSSAM	84.5	36.0	SPODUL	53.2	24.7	PLAGAR	52.3	23.7
4	PISGRA	109.9	31.7	DYSSAM	93.5	34.7	ALPZIZ	39.0	23.8	SYZINO	45.4	23.5
5	DYSSAM	57.0	31.6	DYSSAM	71.8	34.5	SPODUL	67.7	22.6	DYSSAM	65.7	23.4
6	DYSSAM	54.8	30.5	DYSSAM	94.0	32.9	ALPZIZ	33.9	22.0	ALPZIZ	14.4	23.4
7	DYSSAM	77.5	30.4	DYSSAM	84.5	32.4	SPODUL	76.7	21.1	DYSSAM	44.0	23.3
8	DYSSAM	80.5	30.1	DYSSAM	98.9	31.8	DYSSAM	32.3	20.9	ALPZIZ	27.7	23.0
9	FICOBL	n/a	29.7	DYSSAM	93.7	31.5	ALPZIZ	49.4	20.6	SYZINO	57.8	22.9
10	DYSSAM	30.6	27.5	DYSSAM	97.7	31.3	SPODUL	41.7	20.6	ALPZIZ	33.6	22.9
11	DYSSAM	63.6	25.7	DYSSAM	65.9	30.8	ALPZIZ	15.0	20.4	SYZINO	54.1	22.6
12	HERNYM	57.4	25.7	DYSSAM	31.0	29.7	CANODO	39.8	19.9	ALPZIZ	22.6	22.4
13	ARTALT	40.7	25.4	DYSSAM	110.9	29.7	SPODUL	50.0	19.8	SYZINO	40.3	22.1
14	DYSSAM	57.6	25.4	DYSSAM	89.9	29.4	RHUTAI	34.7	19.7	ALPZIZ	39.6	22.0
15	DYSSAM	48.9	25.3	DYSSAM	62.3	28.8	DYSSAM	40.3	19.7	ALPZIZ	38.0	21.8
16	DYSSAM	31.4	25.3	DYSSAM	59.4	28.7	DYSSAM	35.4	19.7	RHUTAI	27.6	21.6
17	ARTALT	25.4	25.2	DYSSAM	73.6	28.5	DYSSAM	28.1	19.6	ALPZIZ	47.0	21.5
18	DYSSAM	34.2	24.8	DYSSAM	99.5	28.2	RHUTAI	61.3	19.2	ALPZIZ	37.3	21.4
19	ARTALT	40.5	24.2	DYSSAM	68.2	28.1	DYSSAM	38.0	19.1	STEFAN	21.8	21.3
20	DYSSAM	37.7	24.2	DYSSAM	93.2	27.7	ARTALT	26.6	18.7	ALPZIZ	20.9	21.3

The Coastal Forest contained the tallest tree of the 6 ha (43.6 m), and there were no other trees >40 m in the 6 ha (Table 5). This single tree could be considered the only true emergent tree in the 6 ha surveyed, because it was more than 5 m taller than the second tallest tree in the plot (Table 5). The set of the eight tallest trees in the Coastal Plantation were not emergents since their heights (30.1 – 32.8 m) were canopy height for the Coastal Forest only 50 m away, and this forest would be expected to revert to a *Dysoxylum*-dominated coastal forest in time. There were no emergent trees in the short-statured upper forest plots.

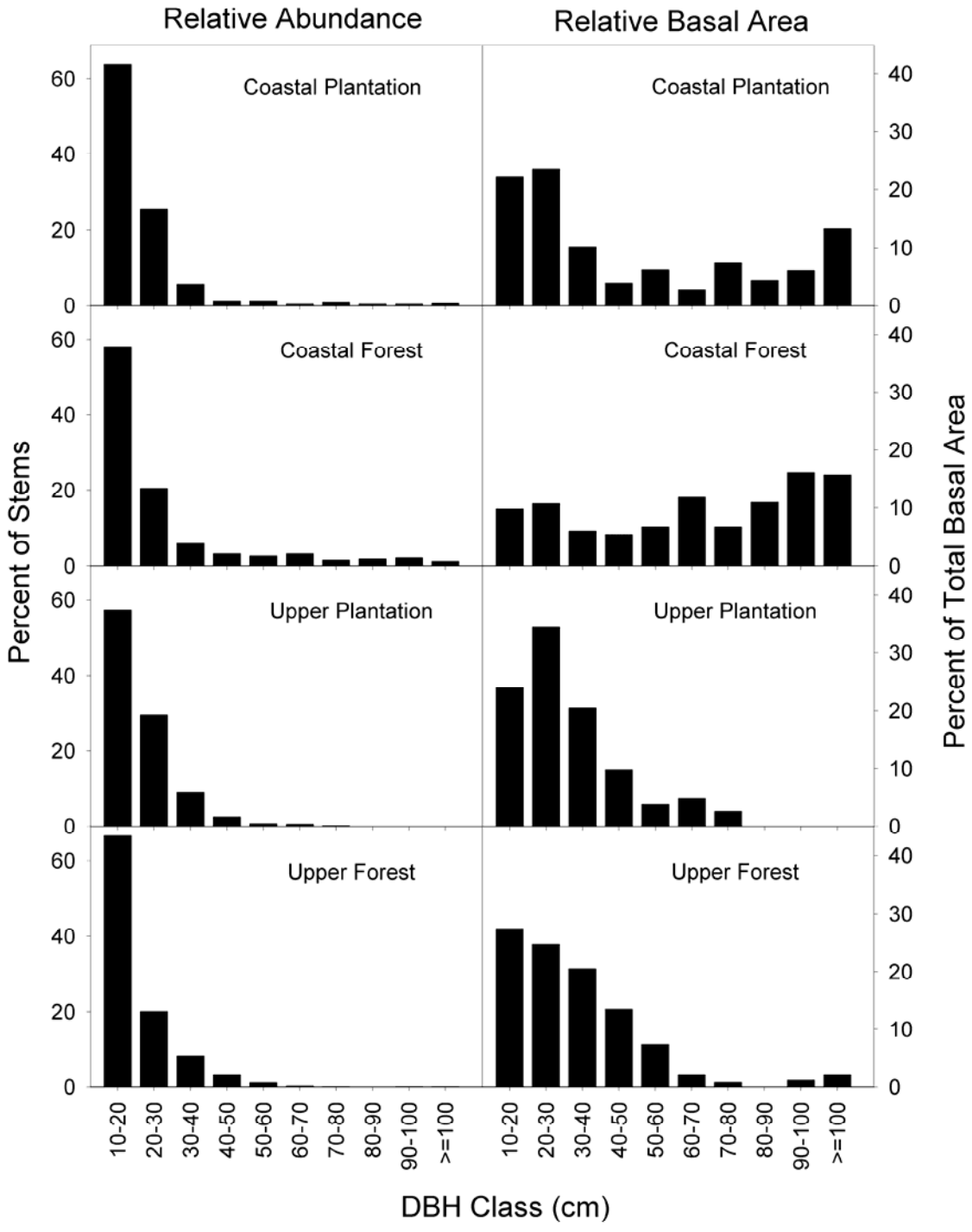
The species composition of the tallest tree group differed among the four plots (Table 5). *D. samoense* contributed greatly to the upper canopy composition of both coastal plots, and was the only species found in the upper canopy of the Coastal Forest. *Pisonia grandis* was an important feature of the upper canopy composition in the Coastal Plantation. In contrast, the tallest trees in the Upper Plantation consisted of the agroforestry species *S. dulcis* and the secondary species *A. zizyphoides*. Only one *D. samoense* tree was among the ten tallest trees in the Upper Plantation. The upper stratum of the Upper Forest canopy consisted primarily of *A.*

zizyphoides and *S. inophylloides*, with *D. samoense* contributing a minor component. Of the six *Planchonella garberi* trees in the Upper Forest, one was among the three tallest trees at that site.

In Figure 7 we compare the size class distributions of the tree communities across the four sites. In general the distribution of size classes was similar across sites, with the exception of the larger tree size classes in the Coastal Forest. In that plot, there was a higher proportion of large trees than in the other three plots. In contrast, the basal area class distributions varied substantially across the four plots (Figure 7). In the Coastal Plantation, the three basal area classes with the greatest contribution to overall basal area were 10 – 20 cm, 20 – 30 cm, and ≥100 cm dbh. In the Coastal Forest, the majority of basal area was contained in trees ≥80 cm dbh, with each class <80 cm dbh contributing similarly. In the Upper Plantation most of the basal area was in trees 10 – 40 cm dbh, and peaking in the 20 – 30 cm dbh class (about 35% total in that class). With no trees above 80 cm dbh in the Upper Plantation, there was no contribution of trees ≥80 cm dbh to plot basal area. The Upper Forest was similar to the Upper Plantation in that the three smallest size classes contributed the greatest to total community basal area, but the 10 – 20 cm dbh class contributed the most to basal area (about 27%). With only two trees ≥80 cm dbh, the contribution of large trees to total community basal areas was minimal.

There was variability in the size class distributions for six common species in the coastal plots (Figure 8). The only species that had similar size class distributions in both coastal sites was *F. scabra*, but this is not surprising because that species rarely achieves large dimensions. It is interesting to note, however, that in the Coastal Forest, we encountered one relatively large *F. scabra* tree of 31.4 cm dbh. The other five species, however, had substantial differences in their size class distributions between the two plots. *Barringtonia asiatica*, *D. samoense*, and *P. grandis* all showed higher numbers of trees 10 – 20 cm dbh in the Coastal Plantation. Moreover, in comparison with the Coastal Forest, *B. asiatica* and *D. samoense* had fewer large trees in the Coastal Plantation. In contrast, *Diospyros samoensis* and *S. fanaiho* had higher numbers of trees 10 – 20 cm dbh in the *Dysoxylum* coastal plot, in addition to greater abundances of larger trees, than in the Coastal Plantation.

Figure 7. Diameter and basal area class distributions for the trees communities of the four permanent forest plots, Ta'u.



Diospyros samoensis is known to be a shade-tolerant and slow growing species that requires long periods of time to reach 10 cm dbh. Our observations have been that seedlings have the capacity to survive in low light levels, and with very slow growth rates. Growth rate data for adult *D. samoensis* trees show that its growth rates are among the slowest of any species in American Samoa (E. Webb, unpublished data). Thus, the recruitment of seedlings into the 10 – 20 cm dbh class takes many years. The higher numbers of *D. samoensis* trees in all size classes in the Coastal Forest therefore suggests that the understory of the Coastal Forest had been subjected to lower intensities of disturbance, and may have had longer to recover from agricultural practices, than the Coastal Plantation.

One rather puzzling result is the difference in size class distributions of *S. fanaiho* between the two coastal plots. It is generally recognized that the Sterculiaceae, along with the closely related Tiliaceae, contain a high proportion of species that can be found in open to disturbed forests. Notwithstanding the fact that Webb and Fa'aumu (1999) found no difference in abundances of *S. fanaiho* among three forest plots on Tutuila (low sample sizes), we would have expected to see higher abundances of *S. fanaiho* in the Coastal Plantation, where light levels were higher. Lack of agreement with our expectation leads us to question whether *S. fanaiho* is an early-successional species that establishes in recently-disturbed forest, or whether it requires a closed secondary forest to be established before seeds can germinate and compete with other species. The fact that large *S. fanaiho* trees can be found in older-growth forest suggests that it is a 'persistent secondary' species. Alternatively, it is possible that seeds are being dispersed into the Coastal Plantation at slower rates than in the Coastal Forest. This could come about as a result of a lack of local seed source or fewer seed deposition events by dispersers (i.e. preference of birds for the Coastal Forest habitat over the Coastal Plantation habitat). Research needs to evaluate the germination and survival requirements of the species.

Six of eight species in the Upper Forest had higher levels of regeneration than the Upper Plantation (Figure 9). *Alphitonia zizyphoides*, *Cananga odorata*, *H. tiliaceus*, *Macaranga stipulosa*, *Rhus taitensis*, and *S. inophylloides* all showed higher numbers of trees in the 10 – 20 cm dbh class than the Upper Plantation. Of those species, all except *Cananga odorata* had more trees in all size classes; 30 – 50 cm dbh *C. odorata* trees were more abundant in the Upper Plantation. In contrast, *B. javanica* and *D. samoense* had more robust populations, with higher levels of 10 – 20 cm dbh trees, in the Upper Plantation than in the Upper Forest.

Figure 8. Size class distributions for important species in the two coastal plots.

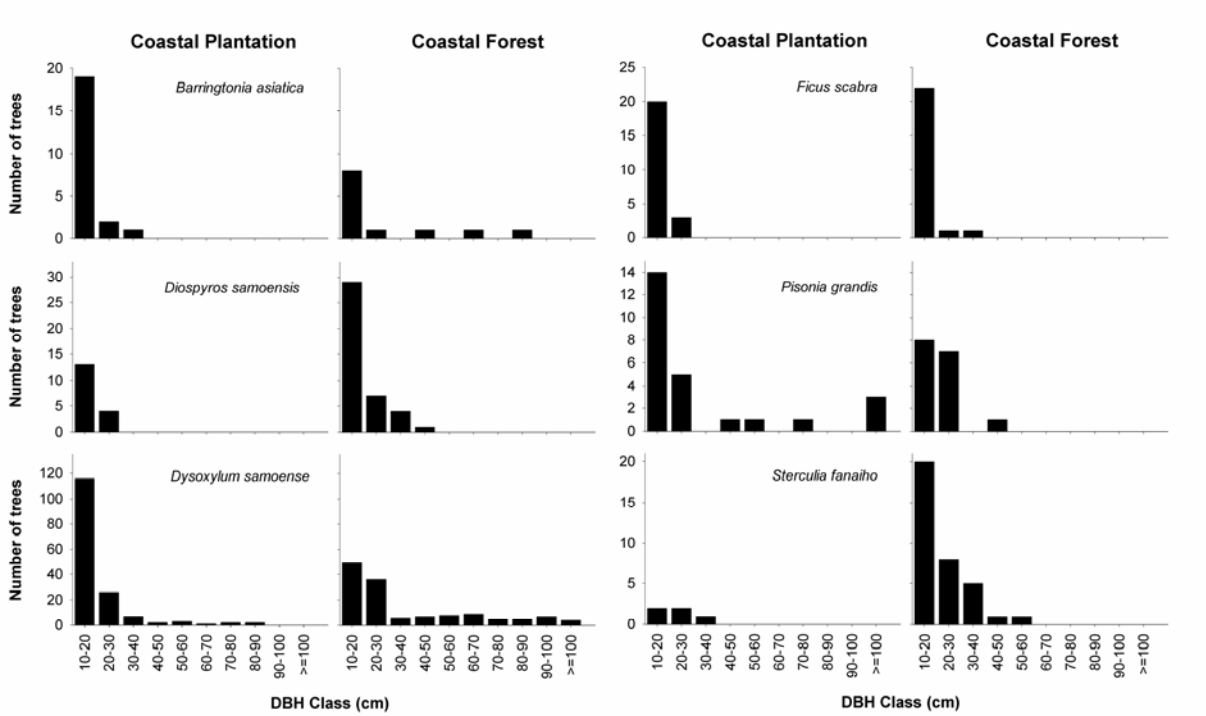


Figure 9. Size class distributions for important species in the two upper plots.

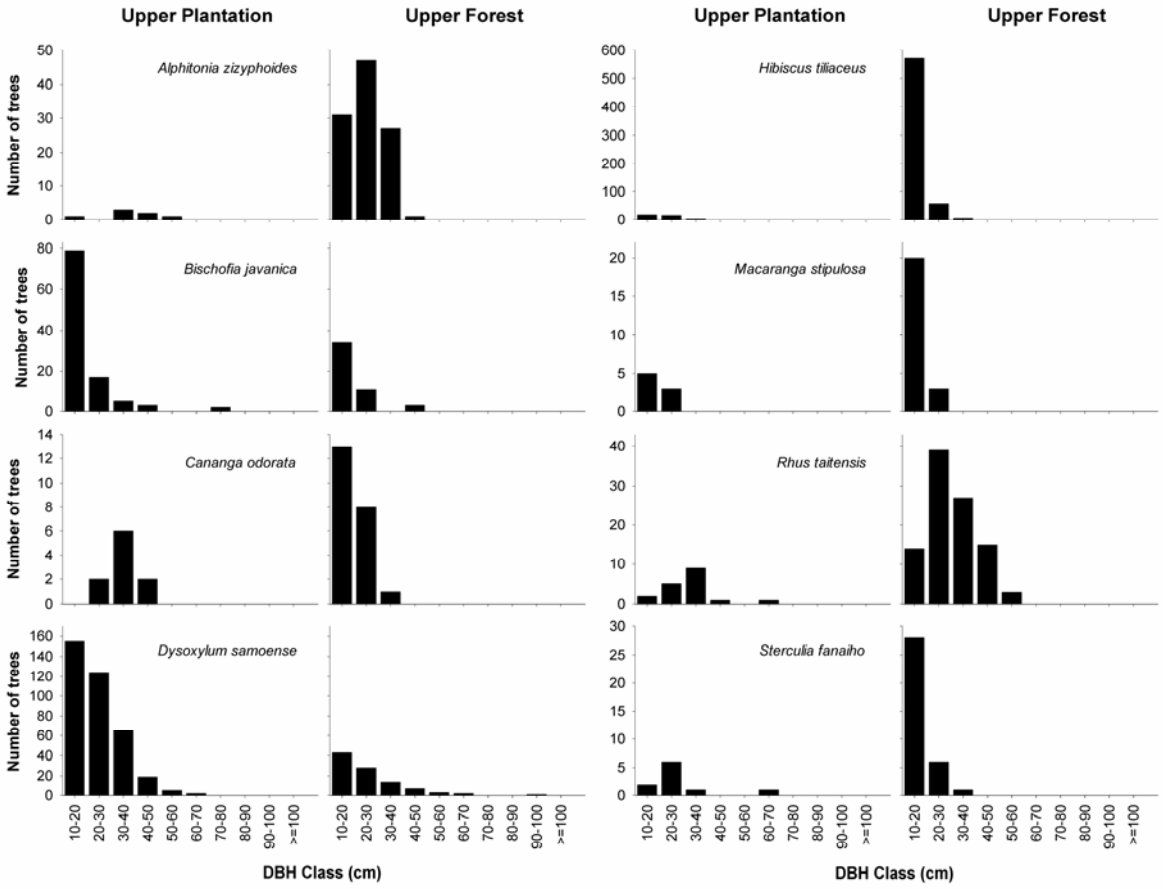


Table 6. Results of spatial analysis calculating Ripley's K for the most abundant species in each plot. The numbers in parentheses indicate the lag distances (m) at which the species exhibited clumping in that plot.

Rank	Coastal Plantation	*Dysoxylum* Coastal Forest	Upper Plantation	Upper Forest
1	*D. samoense* (>1)	*D. samoense*	*A. altilis* (>0)	*H. tiliaceus* (>0)
2	*M. harveyana* (>0)	*D. samoensis*	*D. samoense* (>0)	*M. inutilis*
3	*A. altilis* (>1)	*S. fanaiho* (3-15)	*F. scabra* (1-4)	*A. zizyphoides* (1-30)
4	*C. nucifera*	*P. umbellifera*	*B. javanica* (>9)	*S. inophylloides* (15-35)
5	*F. scabra* (>5)		*M. citrifolia* (>13)	*R. taitensis* (5-25)
6				*D. samoense* (13-32)

These results are different than our expectation based on apparent intensity of disturbance and forest physiognomy in the upper plots. On Tutuila, Webb and Fa'aumu (1999) found higher abundances of *A. zizyphoides*, *B. javanica*, *C. odorata*, *H. tiliaceus*, *M. stipulosa*, and *R. taitensis* in a regenerating forest (Alava) than in mature forest (Amalau or Vatia). On Ta'u, what we considered to be more mature forest had higher abundances of all those species except for *B. javanica*.

Tree dispersion patterns

There was substantial variation between the two coastal plots in the spatial distributions of important species (Table 6, Appendix 2). In the Coastal Plantation, four of the five most common species exhibited clumping at all lag distances (except *F. scabra*, which was not clumped for 1 – 5 m lag distances). In contrast, only *S. fanaiho* exhibited clumping in the Coastal forest, at 3 – 15 m lag distances.

The spatial distribution of abundant species also varied across the two upper plots. In the Upper Plantation, all five of the abundant species were clumped, and the minimum lag distance of clumping increased with species rank (Table 6). In contrast, in the Upper Forest *M. inutilis* exhibited no clumping; however aside from that species a similar trend of increasing minimum lag distance was apparent.

Table 7. Height class distribution of Cyathea *spp. tree ferns in the two upper plots*.

Height (m)	Upper Plantation	Upper Forest
<2.0	0	4
2.0-2.9	1	72
3.0-3.9	1	95
4.0-4.9	0	116
5.0-5.9	0	50
6.0-6.9	1	10
7.0-7.9	0	2
8.0-8.9	0	8
9.0-9.9	3	5
10.0-10.9	2	3
11.0-11.9	0	5
12.0-12.9	1	4
13.0-13.9	0	2
14.0-14.9	0	2
Total	9	378

Tree fern community

Tree ferns were only found in the two upper plots. A total of 388 tree ferns were encountered, of which 379 were in the Upper Forest. In the Upper Plantation, the nine tree ferns ranged in heights, with six of the nine tree ferns greater than 9.0 m. In contrast, of the 378 tree ferns in the Upper Forest, the vast majority was less than 6.0 m tall (Table 7).

The finding that no tree ferns were present in the Coastal Forest was probably due to the substratum in the coastal plots, which was most likely not suitable for *Cyathea*. The large difference in tree fern densities between the Upper Plantation and the Upper Forest plots may have been due to substrata differences, disturbance differences, or a combination of the two. A visual comparison of the spatial maps of *Cyathea* and *H. tiliaceus* in the Upper Forest suggested that there may be a negative association between those two species. Assuming that *H. tiliaceus* is an indicator of past disturbance, then the hypothesis could be generated that *Cyathea* populations are associated with less disturbed forest patches, and therefore less overall-disturbed forests. Further investigation of the tree fern – forest disturbance association should be undertaken in the future.

Forest history, disturbance and condition

The Upper Forest canopy was dominated by *S. inophylloides*, *R. taitensis*, *D. samoense*, and *A. zizyphoides*. *R. taitensis* and *A. zizyphoides* are considered to be dominant early-successional trees (Drake *et al.* 1996, Franklin *et al.* 1999), but *S. inophylloides* is a late-successional species. Thus, despite the lack of evidence for agricultural disturbance, this result confirmed earlier observations (Whistler 1992) that the forests along the eastern slope of Ta'u have been strongly impacted by disturbance and are in a state of succession. The presence of *S. inophylloides* indicates that if left undisturbed, the plot will mature into *Syzygium*-dominated mixed lowland forest (Whistler 1992). Increasing dominance of *S. inophylloides* in later-successional forests may be due to the dense wood of the species, which presumably allows it to persist in hurricane-disturbed forest relatively more successfully than other species (Whistler 1992, Webb *et al*. 1999). Over time, resistance of *S. inophylloides* to hurricanes, when other species would be uprooted, snapped or severely damaged, would allow them to attain canopy stature and become an important canopy component. Given a long enough period of recovery after a cyclone (in this case since Tusi in 1987), structure and diversity could return to more mature-phase conditions.

Variability in composition and structure of the plots reflects the agricultural histories we were able to ascertain from interviews. In the Coastal Plantation, nearly 25% of the relative abundance and relative basal area consisted of *A. altilis* and *C. nucifera*, and in the Upper Plantation *A. altilis* alone comprised 40% of the relative abundance and 32% of the relative basal area. Prolific regeneration of *A. altilis*, which was evident during our field research, served to maintain dominance of this important agroforestry species in former plantations. Monitoring the two plantation plots will reveal the dynamics and compositional changes associated with succession in abandoned plantations (see also Franklin *et al.* 1999).

Cyclones are an important factor in shaping forests of Samoa and Polynesia in general (Elmqvist *et al.* 1994, Elmqvist *et al*. 2001, Hjerpe *et al.* 2001, Franklin *et al.* 2004). Webb *et al.* (1999) found significant differences in canopy height as a function of topography on Tutuila, with well-protected valley forests being significantly taller than exposed ridge forest. The escarpment between the coastal plots and the upper plots is an obvious topographical feature, and could potentially affect the amount of damage sustained by forests during catastrophic events. For example, in Fiji, 72% of the 50 recorded tropical storms (including cyclones) that passed

within 180 nautical miles of Lautoka (Viti Levu) came from the northwest (Brand 2003). Storm trajectory will affect both directionality and force of the winds striking a particular point. In the case of Ta'u it is possible that the coastal plots, which were taller than the upper plots, have been more protected from wind disturbance in the recent past than the upper plots.

Successional development generally results in older forests having greater basal area than younger forests but not necessarily fewer stems (Aide *et al.* 1995, Guariguata and Ostertag 2001, Franklin 2003). In this study, basal area was greater in both forest plots than their corresponding plantation plots. Stem density in the Coastal Plantation was greater than the Coastal Forest, while the Upper Forest had greater stem densities than the Upper Plantation. The high stem densities in the plantations are due to the fact that trees such as *A. altilis*, and *C. nucifera* were already present at the time of abandonment. Indeed, calculating total stem density and basal area in each plot without including those two species dramatically reduces those values. In the Coastal Plantation, stem densities and basal area would be reduced to 348 trees ha^{-1} and 18.2 m^2 ha^{-1}, while the Upper Plantation would be reduced to 353 trees ha^{-1} and 18.3 m^2 ha^{-1}.

Greater overall canopy heights in the forest plots than their corresponding plantation plots may reflect the land management techniques of clearing large trees in heavily disturbed plantation areas. Large trees would be removed for plantations because the root systems and wide crowns would reduce agricultural output. Long-term monitoring of the compositional and structural changes of these plots will reveal the rate at which structural features change over time.

Exotic species in NPSA

Introduced species have become a common feature in the forests of American Samoa, but as yet they are not as threatening to native biodiversity as is the case in other island systems (e.g. Meyer and Florence 1996). Although 99% of all non-native stems in these plots were of species considered not to be a major threat to American Samoa, monitoring and proactive action must take place. For example, we found mature *F. flexuosa* trees in both coastal and upland forest on Ta'u. This species has been widely promoted as a potentially valuable tree in American Samoa for use as building material. The fruits of *F. flexuosa* are favored by several species of birds, including purple-capped fruit doves (*Ptilinopus porphyraceus*) and Pacific pigeons (*Ducula pacifica*) (J. Seamon, Department of Marine and Wildlife Resources, unpublished data).

Therefore, while it is not surprising that *F. flexuosa* escaped into natural forest, it is important to recognize it as a potentially invasive species. Other tree species in American Samoa have been introduced only to naturalize and become aggressive invasives, notably *Adenanthera pavonina*, *Castilla elastica* Cerv., and *Paraserianthes falcataria* (L.) I. Neilsen, the latter of which has been the focus of an intensive eradication program within the National Park of American Samoa. As of yet, there have been no reports of *P. falcataria* on Ta'u, but *C. elastica* has already arrived (E. Webb personal observation). We recommend that *F. flexuosa* be included in the list of potential invasive species for American Samoa. While the plots for this study will give a small sample size of trees to estimate growth rates and possibly localized regeneration, more thorough studies of the growth and regeneration of *F. flexuosa* in native forest of American Samoa are necessary to determine the level of threat posed by this species. At present, the low density of *F. flexuosa* does not make it a high priority for eradication efforts; monitoring of its presence in the forest would, however, be advisable.

Benefits of long-term monitoring for NPSA

Permanent forest plots allow research on the response of vegetation communities to natural disturbances such as hurricanes and human-induced disturbances (e.g. clearing for plantation). The plots we have established, particularly the two plantation plots, will provide unique data on the processes of succession following intensive agriculture and agroforestry activities. These can be compared to the dynamics of the apparently less-disturbed plots of the *Dysoxylum* coastal plot and the Upper Forest. Medium to long-term comparative data could lead to important management recommendations to reduce the level / impact of non-native plantation species in regenerating forest, improve the regeneration of native tree species, or ameliorate negative impacts of potentially invasive species.

Another important benefit of long-term vegetation data is the ability to evaluate forest dynamics within a changing environment. Cyclical changes in weather patterns (such as El Niño) are well documented, and long-term changes in regional weather patterns may also be taking place. Several papers have determined that long-term changes in weather patterns are having measurable impacts on ecosystems. For example, a recent report highlighted the impact of a changing regional climate on the phenology of forest trees in Uganda (Chapman *et al.* 2005). Although American Samoa is a remote island system in the South Pacific, it will not be immune

to climate changes, and is impacted strongly by El Niño. Thus, the plots we have established can contribute to a better understanding of the impacts of climate change on terrestrial ecosystems.

Long-term ecological processes and changes in processes associated with climate change are best measured at the seedling and sapling size classes. Changes in habitat leading to favorable or unfavorable regeneration conditions will first be seen in changes in tree species regeneration. In the plots we established in this project, we only surveyed trees ≥10 cm dbh. It takes decades for small environmental changes to be reflected in changes in the tree community. However, it may take only several years to measure differences in recruitment rates that might be associated with environmental parameters such as an increase or decrease in rainfall. Thus, smaller plots should be established within the larger permanent plots to monitor the regeneration of tree communities from the seed and seedling stage. This will be much more labor-intensive than monitoring the tree community, but will reveal crucial information on the dynamics of the smaller size classes. This could serve as an early-warning system to park management.

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The main field team in the Upper Forest plot. From left to right: Rachel Conejos, Edward Webb, Siaifoi Fa'aumu, Martin van de Bult, Md. Enamul Kabir, Wanlop Chutipong.

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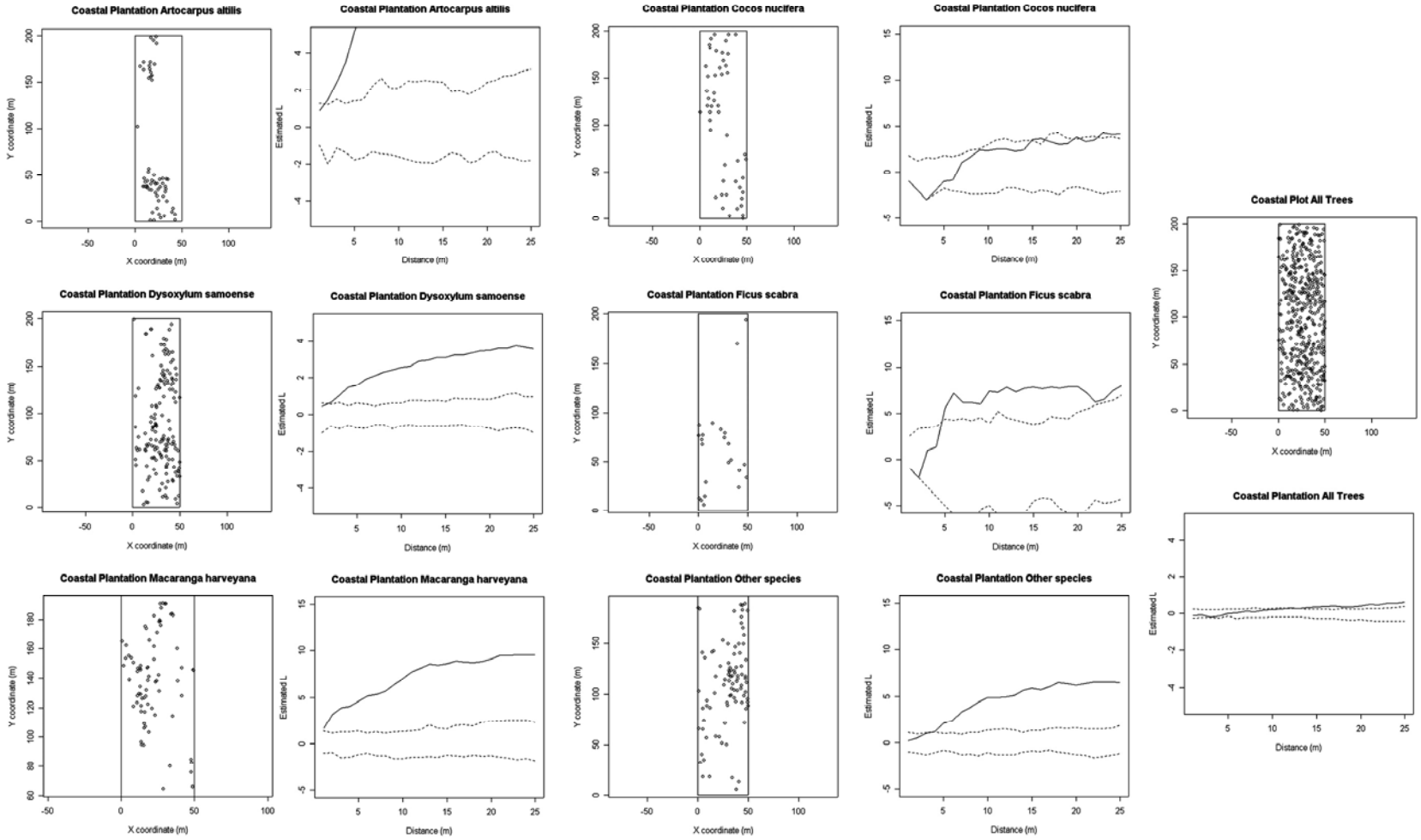
Appendix 1. Summary information for four permanent forest monitoring plots on Ta'u, American Samoa. NO/HA = the number of individuals per hectare, RA = relative abundance, BA / HA = basal area per hectare of all stems, RBA = relative basal area of all stems.

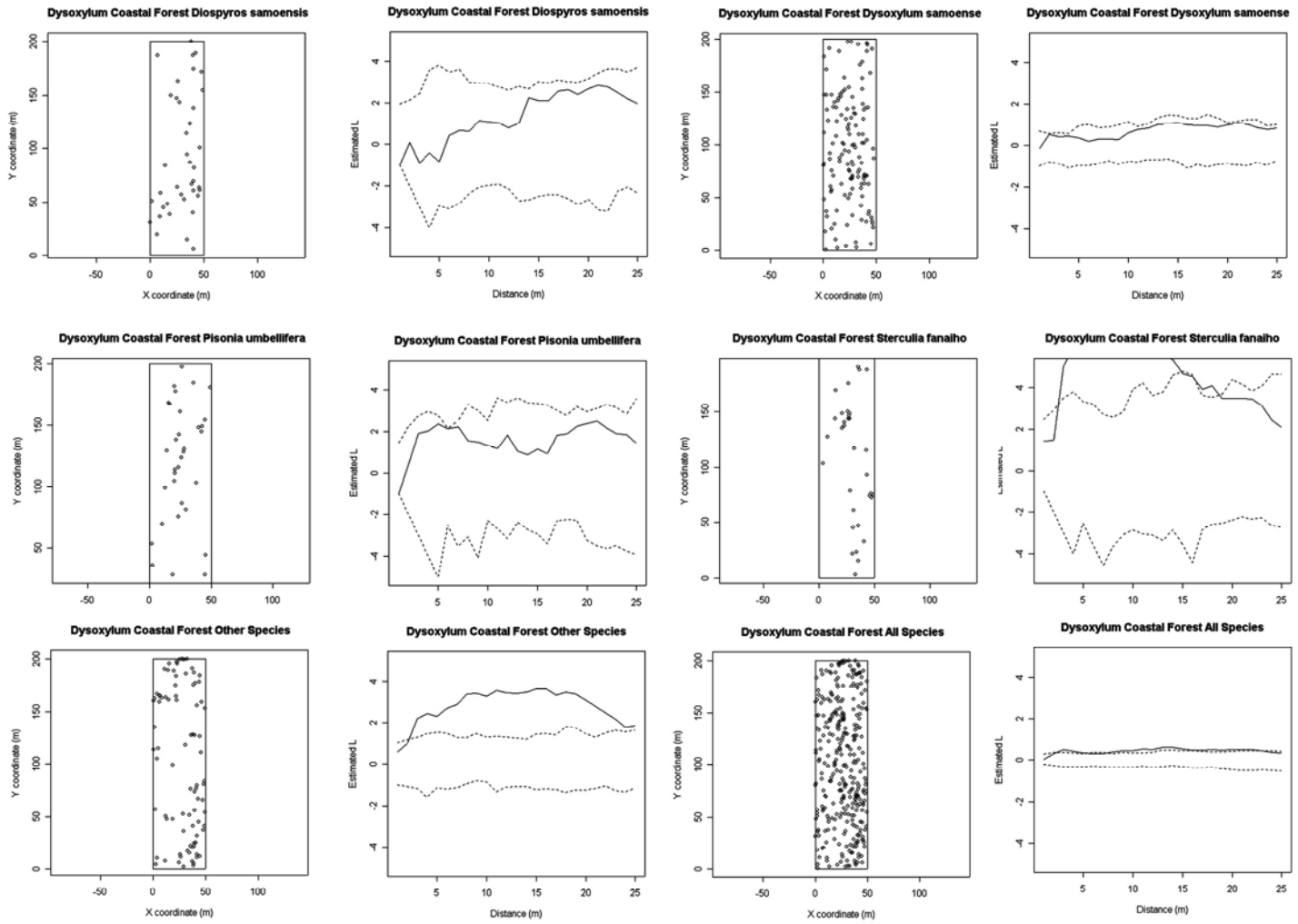
	Coastal Plantation				Coastal Forest				Upper Plantation				Upper Forest				All Plots (6 ha)			
Species	NO / HA	RA	BA / HA	RBA	NO / HA	RA	BA / HA	RBA	NO / HA	RA	BA / HA	RBA	NO / HA	RA	BA / HA	RBA	NO	RA	BA	RBA
Adenanthera pavonina L.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0.5	0.08	0.03	0.10	0.5	0.08	0.01	0.03	2	0.06	0.07	0.04
Aglaia samoensis A. Gray	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1.5	0.24	0.02	0.06	3	0.09	0.03	0.02
Alphitonia zizyphoides (Spreng.) A. Gray	0	0.00	0.00	0.00	0	0.00	0.00	0.00	3.5	0.59	0.44	1.62	51.5	8.13	2.73	9.34	110	3.41	6.35	3.78
Artocarpus altilis (Parkinson) Fosberg	61	13.29	2.99	12.56	0	0.00	0.00	0.00	233.5	39.68	8.82	32.41	0	0.00	0.00	0.00	528	16.35	20.63	12.27
Barringtonia asiatica (L.) Kurz	15	3.27	0.54	2.26	10	3.06	1.31	4.16	0	0.00	0.00	0.00	0	0.00	0.00	0.00	25	0.77	1.85	1.10
Barringtonia samoensis A. Gray	0	0.00	0.00	0.00	0	0.00	0.00	0.00	8.5	1.44	0.11	0.42	0	0.00	0.00	0.00	17	0.53	0.23	0.14
Bischofia javanica Bl.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	36.5	6.20	1.94	7.11	23	3.63	0.80	2.73	119	3.68	5.47	3.25
Calophyllum inophyllum L.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0.5	0.08	0.63	2.15	1	0.03	1.26	0.75
Calophyllum neo-ebudicum Guillaumin	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1	0.16	0.01	0.04	2	0.06	0.02	0.01
Cananga odorata (Lam.) Hook. f. Thoms.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	5	0.85	0.46	1.68	11	1.74	0.33	1.13	32	0.99	1.57	0.94
Canarium vitiense A. Gray	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1	0.16	0.08	0.27	2	0.06	0.16	0.09
Carica papaya L.	1	0.22	0.01	0.06	0	0.00	0.00	0.00	0.5	0.08	0.01	0.02	0	0.00	0.00	0.00	2	0.06	0.02	0.01
Celtis harperi Horne	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1	0.16	0.03	0.12	2	0.06	0.07	0.04
Cerbera manghas L.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	3	0.47	0.12	0.42	6	0.19	0.25	0.15
Cocos nucifera L.	50	10.89	2.59	10.91	0	0.00	0.00	0.00	2	0.34	0.14	0.51	0	0.00	0.00	0.00	54	1.67	2.87	1.71
Crataeva religiosa Forst. f.	1	0.22	0.02	0.08	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1	0.03	0.02	0.01
Diospyros samoensis A. Gray	17	3.70	0.33	1.38	39	11.93	1.22	3.89	0	0.00	0.00	0.00	1.5	0.24	0.02	0.07	59	1.83	1.59	0.95
Dysoxylum samoense A. Gray	157	34.20	7.13	29.98	134	40.98	24.06	76.58	157.5	26.76	9.72	35.71	42	6.63	3.37	11.50	690	21.36	57.37	34.11
Elattostachys falcata (A. Gray) Radlk.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	5.5	0.87	0.14	0.47	11	0.34	0.27	0.16
Elaeocarpus floridanus Hemsl.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	17.5	2.76	0.33	1.14	35	1.08	0.67	0.40
Erythrina variegata L.	0	0.00	0.00	0.00	2	0.61	0.08	0.27	0	0.00	0.00	0.00	0	0.00	0.00	0.00	2	0.06	0.08	0.05
Euodia hortensis Forst.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0.5	0.08	0.01	0.02	1	0.03	0.01	0.01
Ficus obliqua Forst. f.	2	0.44	0.03	0.12	1	0.31	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	3	0.09	0.03	0.02
Ficus scabra Forst. f.	23	5.01	0.41	1.72	24	7.34	0.40	1.28	54	9.18	1.21	4.44	4.5	0.71	0.05	0.16	164	5.08	3.32	1.98
Ficus tinctoria Forst. f.	0	0.00	0.00	0.00	1	0.31	0.02	0.07	0.5	0.08	0.00	0.01	1	0.16	0.01	0.04	4	0.12	0.05	0.03

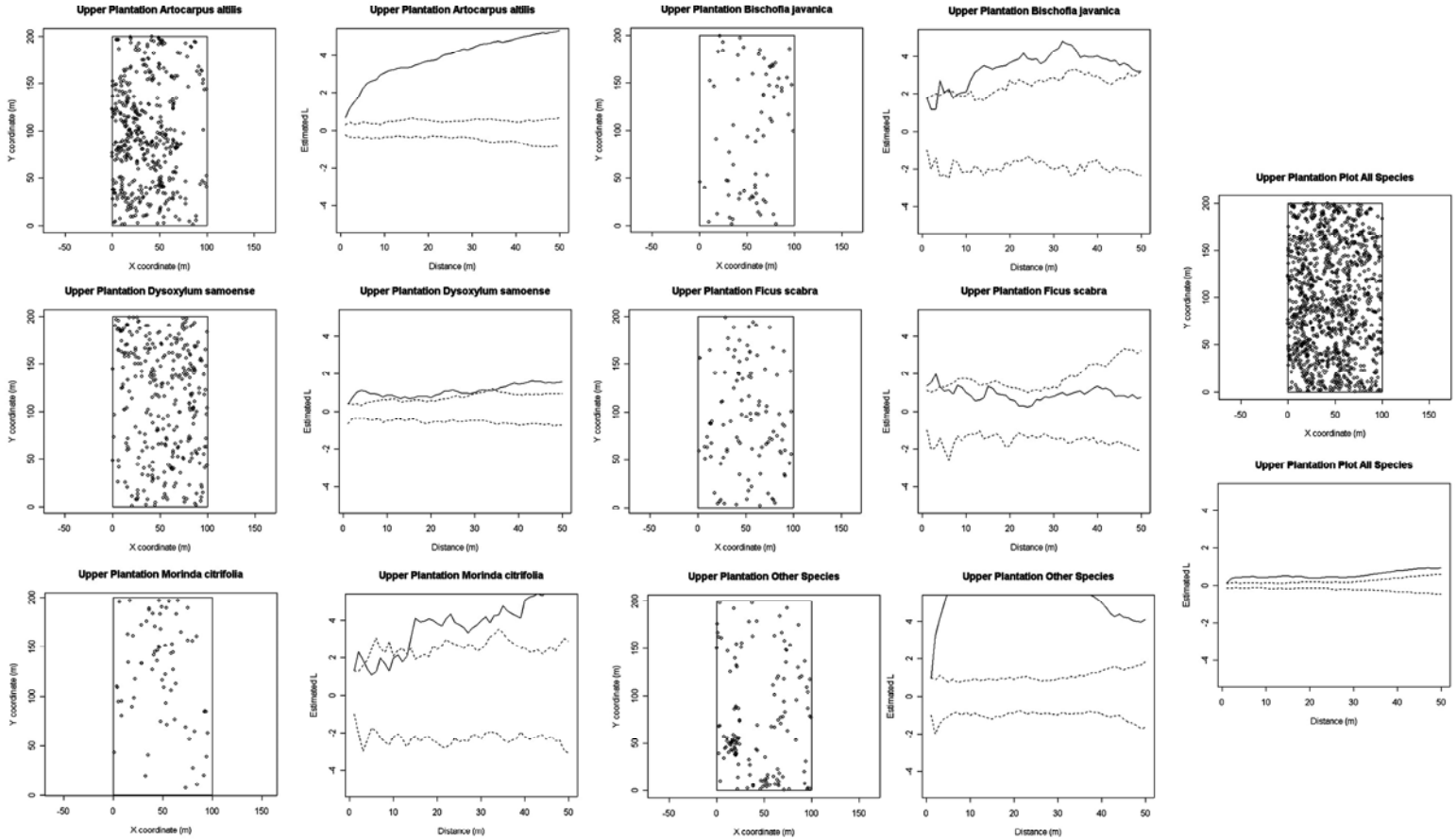
	Coastal Plantation				Coastal Forest				Upper Plantation				Upper Forest				All Plots (6 ha)			
Species	NO / HA	RA	BA / HA	RBA	NO / HA	RA	BA / HA	RBA	NO / HA	RA	BA / HA	RBA	NO / HA	RA	BA / HA	RBA	NO	RA	BA	RBA
Flacourtia rukam Zoll. & Mor. *ex* Mor.	0	0.00	0.00	0.00	1	0.31	0.02	0.05	0	0.00	0.00	0.00	15	2.37	0.26	0.89	31	0.96	0.53	0.32
Flueggea flexuosa Muell. Arg.	9	1.96	0.31	1.32	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1.5	0.20	0.05	0.18	13	0.35	0.42	0.25
Garuga floribunda Decne.	2	0.44	0.04	0.16	8	2.45	0.53	1.69	4	0.68	0.56	2.07	0	0.00	0.00	0.00	18	0.56	1.70	1.01
Glochidion ramiflorum Forst.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	2	0.29	0.08	0.31	3	0.39	0.05	0.18	10	0.27	0.27	0.16
Hernandia nymphaeifolia (Presl.) Kub.	10	2.18	2.93	12.32	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	10	0.31	2.93	1.74
Hibiscus tiliaceus L.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	17	2.89	0.67	2.46	216.5	34.18	5.86	20.02	467	14.46	13.06	7.77
Inocarpus fagifer (Park.) Fosb.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0.5	0.08	0.01	0.02	1	0.03	0.01	0.01
Litsea samoensis (Christoph.) A.C. Smith	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1	0.16	0.05	0.18	2	0.06	0.11	0.06
Macaranga harveyana Muell. Arg.	76	16.56	1.56	6.56	3	0.92	0.07	0.21	0.5	0.08	0.01	0.02	0	0.00	0.00	0.00	80	2.48	1.64	0.97
Macaranga stipulosa Muell. Arg.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1.5	0.25	0.12	0.44	11	1.74	0.21	0.71	25	0.77	0.66	0.39
Meryta macrophylla (Rich) Seem.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	1	0.16	0.01	0.04	2	0.06	0.02	0.01
Morinda citrifolia L.	7	1.53	0.23	0.97	9	2.75	0.13	0.41	35	5.95	0.51	1.87	2	0.32	0.03	0.10	90	2.79	1.44	0.85
Myristica inutilis Rich *ex* A. Gray	0	0.00	0.00	0.00	11	3.36	0.34	1.08	1.5	0.25	0.01	0.05	64	10.10	1.92	6.56	142	4.40	4.21	2.50
Neonauclea forsteri (Seem. *ex* Havil) Merr.	1	0.22	0.00	0.00	2	0.61	0.11	0.34	0.5	0.08	0.06	0.21	15.5	2.45	0.48	1.63	35	1.08	1.17	0.70
Omalanthus nutans (Forst.) Guillemin	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0.5	0.08	0.01	0.02	0	0.00	0.00	0.00	1	0.03	0.01	0.01
Pipturus argenteus (Forst. f.) Wedd.	3	0.65	0.03	0.13	0	0.00	0.00	0.00	9	1.53	0.15	0.54	0	0.00	0.00	0.00	21	0.65	0.32	0.19
Pisonia grandis R. Br.	21	4.58	4.41	18.54	16	4.89	0.62	1.97	0	0.00	0.00	0.00	0	0.00	0.00	0.00	37	1.15	5.03	2.99
Pisonia umbellifera (Forst.) Seem.	0	0.00	0.00	0.00	33	10.09	0.85	2.71	0	0.00	0.00	0.00	0	0.00	0.00	0.00	33	1.02	0.85	0.51
Planchonella garberi Christoph.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	6	0.95	0.68	2.33	12	0.37	1.37	0.81
Pometia pinnata Forst.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	5.5	0.87	0.30	1.01	11	0.34	0.59	0.35
Psydrax merrillii (Setchell) Whistler	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	3	0.47	0.07	0.23	6	0.19	0.13	0.08
Rhus taitensis Guillemin	0	0.00	0.00	0.00	0	0.00	0.00	0.00	5.5	0.93	0.83	3.03	44.5	7.02	3.92	13.38	100	3.10	9.49	5.64
Spondias dulcis Forst.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	3.5	0.59	0.98	3.61	0	0.00	0.00	0.00	7	0.22	1.97	1.17
Sterculia fanaiho Setchell	3	0.65	0.22	0.92	33	10.09	1.67	5.30	5	0.85	0.34	1.25	17.5	2.76	0.37	1.27	81	2.51	3.31	1.97
Syzygium malaccense Merr. & Perry	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0.5	0.08	0.01	0.03	0	0.00	0.00	0.00	1	0.03	0.02	0.01

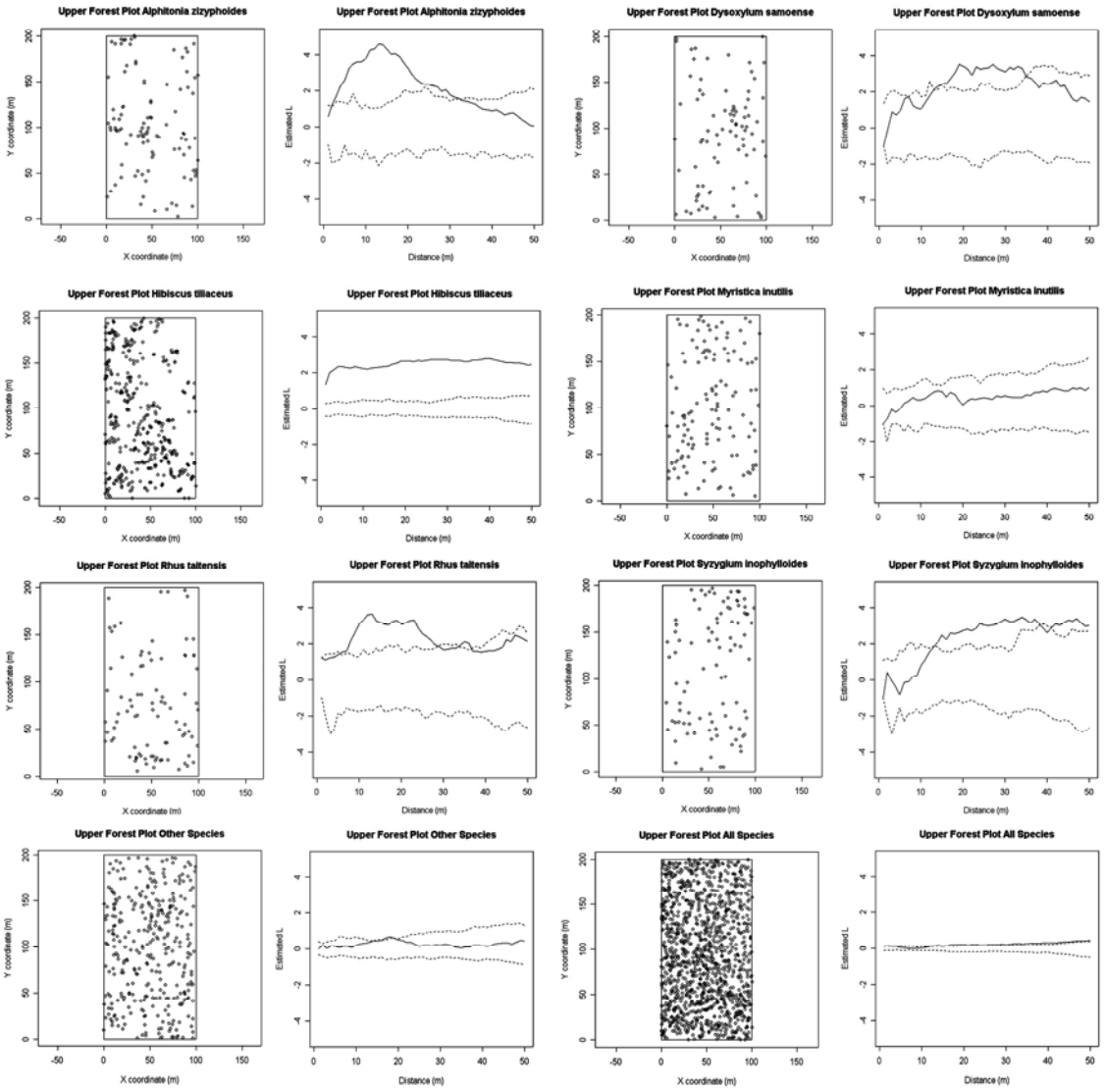
	Coastal Plantation				Coastal Forest				Upper Plantation				Upper Forest				All Plots (6 ha)			
Species	NO / HA	RA	BA / HA	RBA	NO / HA	RA	BA / HA	RBA	NO / HA	RA	BA / HA	RBA	NO / HA	RA	BA / HA	RBA	NO	RA	BA	RBA
Syzygium inophylloides (A. Gray) C. Muell.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	47	7.42	5.49	18.74	94	2.91	10.97	6.52
Syzygium samarangense (Bl.) Merr. & L.M. Perry	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	2	0.32	0.03	0.10	4	0.12	0.06	0.03
Trema cannabina Lour.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0.5	0.08	0.01	0.04	0	0.00	0.00	0.00	1	0.03	0.02	0.01
Trichospermum richii (A. Gray) Seem.	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0	0.00	0.00	0.00	10.5	1.66	0.81	2.77	21	0.65	1.62	0.96
Sum	459		23.78		327		31.42		588.5		27.23		633.5		29.27		3230		168.20	
Number of species	18				16				26				35				54			

Appendix 2. Output of spatial analysis calculating Ripley's K for various lag distances of common species for each plot. For each graphical pair, the left figure is the map of that species in the plot, and the right graph shows Ripley's K value across lag distances. The dotted lines represent the calculated maximum and minimum values of Ripley's K for that lag distance in the plot and the dark line represents the actual K value for the species in the plot. Where the dark line is outside the maximum or minimum values indicates significant clumping (if above the maximum value) or significant hyperdispersion (if below the minimum value).


Coastal Plantation Artocarpus altilis
Y coordinate (m)
X coordinate (m)
Coastal Plantation Artocarpus altilis
Estimated L
Distance (m)
Coastal Plantation Cocos nucifera
Y coordinate (m)
X coordinate (m)
Coastal Plantation Cocos nucifera
Estimated L
Distance (m)
Coastal Plot All Trees
Y coordinate (m)
X coordinate (m)
Coastal Plantation Dysoxylum samoense
Y coordinate (m)
X coordinate (m)
Coastal Plantation Dysoxylum samoense
Estimated L
Distance (m)
Coastal Plantation Ficus scabra
Y coordinate (m)
X coordinate (m)
Coastal Plantation Ficus scabra
Estimated L
Distance (m)
Coastal Plantation All Trees
Estimated L
Distance (m)
Coastal Plantation Macaranga harveyana
Y coordinate (m)
X coordinate (m)
Coastal Plantation Macaranga harveyana
Estimated L
Distance (m)
Coastal Plantation Other species
Y coordinate (m)
X coordinate (m)
Coastal Plantation Other species
Estimated L
Distance (m)


Dysoxylum Coastal Forest Diospyros samoensis
Y coordinate (m)
X coordinate (m)
Dysoxylum Coastal Forest Diospyros samoensis
Estimated L
Distance (m)
Dysoxylum Coastal Forest Dysoxylum samoense
Y coordinate (m)
X coordinate (m)
Dysoxylum Coastal Forest Dysoxylum samoense
Estimated L
Distance (m)
Dysoxylum Coastal Forest Pisonia umbellifera
Y coordinate (m)
Dysoxylum Coastal Forest Pisonia umbellifera
Estimated L
Dysoxylum Coastal Forest Sterculia fanaiho
Y coordinate (m)
Dysoxylum Coastal Forest Sterculia fanaiho
Dysoxylum Coastal Forest Other Species
Y coordinate (m)
X coordinate (m)
Dysoxylum Coastal Forest Other Species
Estimated L
Distance (m)
Dysoxylum Coastal Forest All Species
Y coordinate (m)
X coordinate (m)
Dysoxylum Coastal Forest All Species
Estimated L
Distance (m)


Upper Plantation Artocarpus altilis
Upper Plantation Artocarpus altilis
Upper Plantation Bischofia javanica
Upper Plantation Bischofia javanica
Upper Plantation Plot All Species
Upper Plantation Dysoxylum samoense
Upper Plantation Dysoxylum samoense
Upper Plantation Ficus scabra
Upper Plantation Ficus scabra
Upper Plantation Plot All Species
Upper Plantation Morinda citrifolia
Upper Plantation Morinda citrifolia
Upper Plantation Other Species
Upper Plantation Other Species
Y coordinate (m)
X coordinate (m)
Estimated L
Distance (m)


Upper Forest Plot Alphitonia zizyphoides
Upper Forest Plot Alphitonia zizyphoides
Upper Forest Plot Dysoxylum samoense
Upper Forest Plot Dysoxylum samoense
Upper Forest Plot Hibiscus tiliaceus
Upper Forest Plot Hibiscus tiliaceus
Upper Forest Plot Myristica inutilis
Upper Forest Plot Myristica inutilis
Upper Forest Plot Rhus taitensis
Upper Forest Plot Rhus taitensis
Upper Forest Plot Syzygium inophylloides
Upper Forest Plot Syzygium inophylloides
Upper Forest Plot Other Species
Upper Forest Plot Other Species
Upper Forest Plot All Species
Upper Forest Plot All Species
Y coordinate (m)
X coordinate (m)
Estimated L
Distance (m)